The 'Mosaic habitat' concept in human evolution: Past and present.

Sally C. Reynolds [a], David M. Wilkinson [b], Christopher G. Marston [b] and Hannah J. O'Regan [a]

Author affiliations:

[a] Department of Archaeology, Humanities Building, University Park, University of Nottingham, NG7 2RD, UK.

[b] School of Natural Sciences and Psychology, James Parsons Building, Byrom Street, Liverpool L3 3AF, UK

Running head: Mosaic habitats in human evolution

Corresponding author: Hannah O'Regan, Email: Hannah.o'regan@nottingham.ac.uk

KEY WORDS: Habitat heterogeneity; time-averaging, habitat variability, Savannah Hypothesis, palaeoenvironmental reconstruction; palaeoecology,

Abstract

The habitats preferred by hominins and other species are an important theme in palaeoanthropology, and the 'mosaic habitat' (also referred to as habitat heterogeneity) has been a central concept in this regard for the last four decades. Here we explore the development of this concept – loosely defined as a range of different habitat types, such as woodlands, riverine forest and savannah within a limited spatial area– in studies of human evolution in the last sixty years or so. We outline the key developments that took place before and around the time when the term 'mosaic' came to wider palaeoanthropological attention. To achieve this we used an analysis of the published literature, a study of illustrations of hominin evolution from 1925 onwards and an email survey of senior researchers in palaeoanthropology and related fields. We found that the term mosaic starts to be applied in palaeoanthropological thinking during the 1970's due to the work of a number of researchers, including Karl Butzer and Glynn Isaac , with the earliest usage we have found of 'mosaic' in specific reference to hominin habitats being by Adriaan Kortlandt (1972). While we observe a steady increase in the numbers of publications reporting mosaic palaeohabitats, in keeping with the growing interest and specialisation in various methods of palaeoenvironmental reconstruction, we also note that there is a lack of critical studies that define this habitat, or examine the temporal and spatial scales associated with it. The general consensus within the field is that the concept now requires more detailed definition and study to evaluate its role in human evolution.

Introduction

In 1965 the distinguished ecologist G. Evelyn Hutchinson published a book of his collected essays entitled '*The Ecological Theater and the Evolutionary Play*' (Hutchinson, 1965). His title neatly captures the idea that the environment (ecology) sets the context for evolutionary change, an idea that was completely mainstream in mid-20th century science. Such interactions have had a prominent role in studies of human evolution in the mid to late 20th century – a well-known example being the Savannah Hypothesis (Bender *et al.*, 2012; Domínguez-Rodrigo, 2014). However the role of the environment, and particularly adaptation to the environment, played a lesser role in theories of human evolution in the 19th and first half of the 20th Century when there was often an emphasis on inbuilt evolutionary drives towards certain goals and an assumption that human features, such as bipedalism, were so obviously advantageous that they required little explanation (Bowler, 1986). As Bowler (1986) pointed out, it was the increased emphasis on adaptations that arose from the 'new', or 'modern' evolutionary synthesis (mainly between 1936 and 1947 (Mayr, 1980)), that started to make more mainstream the narratives of human evolution which put significant emphasis on environmental adaptations. Although an increased interest in such questions started around the 1930s, as so often in science it is possible to find a number of interesting precursors. For example as far back as Lamarck (1809) and Darwin (1871), naturalists have made at least passing references to the importance of the type of habitats our early ancestors lived in and the role that this may have played in our evolution. Lamarck is a particularly interesting example – although his comments on the selection pressures leading to bipedalism are restricted to less than a page he produced what Mayr (1982, p352) described as a "startlingly modern" suggestion about the role of potential habitat change in the evolution of a bipedal stance. More recently placing

hominins within a distinct habitat type, against the backdrop of shifting African Pliocene and Pleistocene climates and environments, has been an important goal of palaeoanthropology (Butzer, 1977; Potts, 1998; 2013; deMenocal 1995, 2004, 2011; Bobe and Eck, 2001; Bobe, 2006; Kingston *et al*., 2007; Reed, 1997, 2013). Several different habitat scenarios exist, including the Savannah Hypothesis, the Forest Hypothesis, the Turnover Pulse Hypothesis, the Variability Selection Hypothesis, the Tectonic Landscape Model and others (Dart, 1925; Vrba, 1980; Potts, 1998; 2013; Retallack, 2001; Kingston, 2007; Trauth *et al*., 2010; Reynolds *et al*., 2011; Bender *et al*., 2012; Domínguez-Rodrigo, 2014). One of the reasons for this multiplicity of hypotheses (in addition to it being unlikely that there is one 'correct' answer) is that the environmental evidence is being viewed in very different ways. A recent review of the place of the 'Savannah Hypothesis' in human evolution studies by Domínguez-Rodrigo, (2014) clearly shows that part of the problem lies with imprecise definitions of vegetation states that lie on a continuum, where the term 'savannah' could equally denote pure grasslands or mosaic habitats where a significant amount of trees is present in grasslands (Fig 1). Therefore, there is a degree of overlap between the vegetation referred to here as 'mosaic habitats' and some of the habitats described in the Savannah Hypothesis.

The 'Mosaic Habitat' is deserving of particular attention because over the last few decades it has been reconstructed at many hominin sites across Africa from various types of palaeoenvironmental evidence (Table 1) and the use of the term in published literature is increasing, as we demonstrate later. To our knowledge a formal palaeoenvironmental definition of 'Mosaic Habitat' does not exist, but it may well have developed out of the older, more established, Savannah Hypothesis – which often emphasised extensive grassland habitats (Domínguez-Rodrigo, 2014). A typical working definition of a mosaic habitat is as follows: "a range of different habitat types, scattered across and interspersed within a given

area" (Elton, 2008:381). Perhaps surprisingly, given its modern ubiquity, this term only appears in the palaeoanthropological literature in the 1970s (see below). In the four decades since then, the term has become more widely used, so much so, that recent literature has started to expand the application of mosaics in human evolution from Africa to more recent hominin taxa – such as those in Eurasia (Finlayson, 2009; Finlayson *et al*., 2011).

An early usage is seen in Glynn Isaac's (1976:501) chapter in "*Human Origins: Louis Leakey and the East African Evidence*", in which he described the attractive nature of the "diversity of resources" offered by the "mosaic of diverse habitats" at Omo and Koobi Fora (in Ethiopia and Kenya), and it still remains central to our perceptions of human evolution, as illustrated by the following recent quotation: ''The cradle of humanity was …in the savanna forest, favoured by its complex mosaic of different local habitats" (Wilson, 2012:29). However, certain researchers have begun to voice the opinion that as a habitat concept, the mosaic is too general to be informative (Kingston, 2007).

Here we review the origin and development of the 'mosaic habitat' in human evolution studies. As the word 'mosaic' suggests, this habitat concept implies several different vegetation types arranged in patches within a delimited area. Focusing on a particular word – in this case 'mosaic' – could be seen as less than ideal as it is the idea (the importance of habitat heterogeneity) rather than the word itself that is important. However as Gould (2002:875) pointed out, words matter as 'phenomena without names, and theories marking them as worthy of notice, will probably not be recognised at all'. While mosaic is the most frequently encountered term, we here consider the words heterogeneous, mixed and patchy as synonyms for similar vegetation distributions. Habitat heterogeneity is clearly important in palaeoanthropology, but this concept requires more in-depth research than it has currently received. Calls for more explicit definitions of habitats are not new: indeed

Irwin Bernstein (1967: 178) specifically mentioned the lack of spatial and temporal scales in definitions of natural habitats in the 1960s.

For the purposes of our review, we outline the key developments that took place before and around the time when the term 'mosaic' came to wider palaeoanthropological attention. To achieve this we use several strands of evidence, including published research (online and print-based, summarized in Table 2), artistic representations of early hominin reconstructions, and focused questions to senior academics in palaeoanthropology and primatology, many of whom were students during the time period in which mosaics became incorporated into human evolution studies (Table 3). Such survey-based data potentially add important historical information about the use of the concept outside of published literature (See Glen, 1994; Sapp, 2009, for the use of this approach in other areas in the history of science), as there may be time lags between an idea being informally discussed and it appearing in publications. In addition to which, scientific papers are often uninformative when it comes to articulating the original genesis of the ideas they discuss (Medawar, 1963) making such an oral history approach potentially very valuable.

Mosaics in a wider context - a brief history of mosaics in the ecology literature

Our intention with this paper is not to review the use of the concept of habitat mosaics across all of evolutionary biology and ecology, but to focus particularly on the area of human evolution. However because the term has been widely used in plant ecology we first briefly review the more conventional ecological usage before focusing on human evolution in African environments. The term 'mosaic vegetation' was first used in plant

ecology over 100 years ago (e.g. Pound and Clements, 1897; Cavers, 1914), but it was not until the 1940s that mosaic became a commonly applied idea (e.g. Watt, 1947; McIntosh, 1999). For example, vegetation mosaics were given particular prominence in the work on plant community ecology by R.H. Whitaker from the 1950s onwards (Kent, 2011). The term is still widely used in ecology today (e.g. Soininen *et al*., 2013; Fonderflick *et al*., 2013; Campioni *et al*., 2013; Marimon *et al.*, 2014) and the current importance given to ideas of metapopulations and spatial dynamics in ecology makes patchy habitats of particular interest (Nee, 2007). In addition the rise in landscape ecology as a discipline over the past 25 years has also given a particular prominence to mosaics, as landscapes are often viewed as composed of a variety of patches of different vegetation types (Kent, 2011).

Several scientists with field naturalist backgrounds who also have an interest in human evolution (especially Jonathan Kingdon and Edward O. Wilson (pers. comms.)) pointed out to us that mosaics are a fairly obvious concept for any naturalist who works in a part of the world where vegetation is not found in large uniform blocks. We are aware of no formal definition of 'mosaic' in the ecological literature, but the generally accepted ecological usage suggests at least two types of vegetation that are distributed across a landscape. There are exceptions to this definition: if two types of vegetation meet along a gradient (e.g. a solid block of woodland meeting a solid patch of grassland), then this is usually referred to as an ecotone, rather than a mosaic (Calow, 1999).

Early 20th century descriptive studies of African vegetation, in particular in eastern Africa, make frequent mention of the mosaic-like nature of the vegetation (Michelmore, 1934, 1939; Vesey-Fitzgerald, 1963); later ecological studies focused on the mechanisms that create and stabilise mosaics, such as grazing by herbivores and fire (Belsky, 1986; Bond and Keeley, 2005; Sinclair, 2012). There are interesting parallels between the term 'mosaic' and

'savannah' in the ecological literature. As with mosaic, savannah is a term widely used by plant ecologists that also lacks a widely-agreed formal definition (Torello-Raventos *et al*., 2013).

Development of the Mosaic Concept within human evolution studies

Firstly we briefly review the development of this idea before describing the results of different lines of historical evidence (visual reconstructions, focussed questions and text-based sources) to studying the history of the mosaic concept in palaeoanthropology. We then draw these lines of evidence together into a more detailed history of the development of the concept during the late 20th century.

Although Wells *et al.* (1931), in a popular encyclopaedia of biology, briefly raised the possible importance of forest/open country ecotones in the context of human evolution most early palaeoanthropological studies largely focused on the hominin fossils, as well as the comparative anatomy of primates, in order to clarify taxonomic affinities of the hominins (Elliot Smith, 1924; Dart, 1925; Le Gros Clark, 1959a). Other important foci included dating the early sites and their faunas and establishing relative chronologies (e.g. Clark, 1957; Bishop and Miller, 1972). In the context of Wells *et al.* (1931) suggestion it is probably relevant that one of the authors was Julian Huxley – a key player in the evolutionary synthesis of the late 1930's and early 1940's and actively thinking about the role of selection in relation to the environment (Bowler 1986). Reviews of progress in the field of palaeoanthropology by Le Gros Clark (1967), Leakey and Goodall (1970), Cartmill *et al*., (1986), Tattersall (2000) and Goodrum (2013) clearly highlight these early goals, but make no detailed mention of the environmental context for hominin evolution. Indeed, Karl Butzer in the preface to his book *Environment and Archaeology* (1971: vii) wrote "In preparing the

original version of this book [published in 1964] I made an explicit plea for a Pleistocene geography concerned with man and the land. This revised edition reflects my concern that dating techniques, geomorphological theory, and regional stratigraphy continue to be overemphasized in the literature and in the classroom, with insufficient stress on the total environment." The fact that Butzer was trained as a geographer is obviously relevant to understanding why he came to consider this aspect of human evolution important and understudied.

Notable early exceptions to this lack of an environmental perspective are the works of Basil Cooke, Lawrence Herbert Wells and Ronald Singer who, in the 1950s, were using fossil fauna to attempt to reconstruct the past environments at several South African sites. Singer (1957:178) wrote of Elandsfontein that the "site represents the desiccated basin of a prehistoric marshy vlei (lake or pool) surrounded by grassy plains and hills in which fairly dense scrub bushes and leafy trees must have been prominent features." While for the site of Makapansgat, Wells and Cooke (1956:48) made a link between the "great wealth of species" observed for the fossil antelopes and the "physiographic setting of the site in a scrub-covered mountain mass, with extensive open or bush-covered plains at no great distance". Both descriptions would probably be termed mosaic today.

Thus, until the mid-1970s the term 'mosaic habitat' occurred infrequently in the palaeoanthropological literature, but the appreciation of the role of mixed, heterogeneous, habitats was being established from the 1950s onwards. Gradually, the perspective altered to encompass detailed environmental and climatic reconstructions and evaluation of the role played by environments in shaping the course of human evolution; a trend still very much in evidence today (e.g. Cooke, 1978; Peters, 1979; deMenocal, 1995; 2004; Potts, 1998; 2013 and others). Bernard Campbell's textbook *Human Evolution, an introduction to*

man's adaptations, aptly illustrates this shift. A subsection entitled 'leaving the forest' in the 1967 edition makes almost no mention of habitats except as a substrate for hominin movement, while the 1974 second edition has a paragraph inserted at the start of the same subsection that explicitly mentions an 'ecotone' (Campbell, 1974: 376).

Artistic reconstructions

Illustrations can be highly influential in communicating ideas in science (e.g. Rudwick, 1976), therefore artistic attempts to portray hominins provide additional insights into changing perceptions of past environments, as an illustrator is forced to make a deliberate choice about what to show – while a verbal description can more easily miss out whole aspects of a scene. Although it may be tempting to see such images as objective illustrations of the science of the time they can clearly be influenced by a wide range of other cultural, artistic and commercial influences (Privateer, 2005), so they need interpreting with caution and in the context of other lines of evidence.

Darwin's early speculations on human evolution included an African origin and upright stance predating later increases in intelligence and brain size. He suggested a possible environmental context for the switch to a bipedal stance – namely increasing terrestrial locomotion and use of habitats away from dense forest although he conceded that this could just have plausibly led to improvements in quadrupedal locomotion too (Darwin, 1871; Bowler, 1986, 2003). However, until well into the 20th century Africa was largely seen by most workers as irrelevant to the key developments in human evolution. Instead, much attention focused on Europe and later Asia following the discovery of the first *Pithecanthropus* (later renamed *Homo erectus*) fossils (Bowler, 2003). Indeed many of the earlier versions of the savannah hypothesis envisaged our ancestors evolving in the

grasslands of central Asia (Bowler, 1986; Bender *et al.*, 2012). Only some years after the discovery of *Australopithecus africanus* (Dart, 1925) did the potential importance of African savannah habitats start to become apparent.

Many of the key early 20th century texts, such as Keith (1925), focus almost exclusively on the anatomy of the fossils and with little discussion of the potential ecological context. A similar trend is mirrored in the artistic representations of the period. Once *Australopithecus africanus* had been announced to the world, reconstructions began to appear in popular publications. These early reconstructions tended to be vignettes of just the head of the hominin, with no environment (Fig. 2), or had the reconstructed hominin dominating the picture with only very limited landscape visible (Fig. 3). Classic early 20th century examples of this style include the work of artist Charles R. Knight (Milner, 2012).

These illustrations reveal the focus on anatomy, but also reflect a concomitant lack of palaeoecological context for the early excavations at African sites, such as Olduvai Gorge, Tanzania. Louis Leakey's remarks in *Olduvai Gorge* Volume 1 reveal a reluctance to determine habitats based on the data available to him at the time: "While we may justifiably conclude that the presence of fish, hippopotamus, crocodiles and aquatic birds indicates the presence of a relatively stable body of water, it is necessary to use great caution when attempting to assess climatic conditions on the basis of most mammals" (Leakey, 1965:74). In contrast, the presence of fruits and seeds in the Miocene deposits at Rusinga Island (Kenya) meant that habitat reconstructions for this earlier period were being created and discussed much earlier than those of *Australopithecus* and early *Homo*. For example, the Miocene taxa *Proconsul* and *Limnopithecus* (now known as *Dendropithecus*) were described as being "found in association with fossil faunal and floral assemblages that showed these creatures had once lived in open grasslands, between forest galleries, along the rivers which

once flowed into an ancient Miocene lake" (Leakey, 1960: 18). Therefore the relative lack of non-faunal habitat indicators (such as plant remains) may have hindered palaeoecological research at Pliocene and Pleistocene sites for some time.

Despite this lack of palaeoecological data, by the 1950s colour illustrations were being produced for the British Museum (Natural History) by Maurice Wilson that are still being used today in a non-historical context (e.g. Andrews and Stringer, 1989; Stringer and Andrews, 2005). Figure 4 shows a reconstruction of *Australopithecus africanus* in a rocky landscape, but with distinctively African Euphorbias in the background – an example of modern African ecology standing in for missing palaeoecological information (taken to its extreme in Edey (1973) where drawings of hominin reconstructions are inserted into photographs of modern African landscapes).

By the later 1950s, Neave Parker had created an 'active' reconstruction for hominins at Olduvai Gorge, using information supplied by Louis Leakey on the recently discovered Chellean (Early Stone Age) living floor and fauna (Leakey, 1957, 1958; and see de la Torre, 2011). This 1958 illustration (Fig. 5) is a mosaic in all but name, showing bushland, grassland and water. By the mid-1960s Jay Matternes' hominin dioramas, as seen in Howell (1970), show hominins in highly variable environments, although mosaics are not explicitly mentioned in Howell's text. In E. O. Wilson's (1975) influential text *Sociobiology, the new synthesis* his fig 27-5 shows a reconstruction of a group of *Homo habilis* in a mosaic landscape – drawn by Sarah Landy (the text credits F. Clark Howell with providing advice on the reconstruction). However the text makes no explicit reference to the mosaic landscape and Wilson (pers. comm.) says he only gave serious thought to the role of mosaics in human evolution while researching his much later book '*The social conquest of Earth*' (Wilson, 2012).

It is possible that the illustrations of variable or mosaic habitats in popular science books and the press, played a role in communicating the idea of the mosaic habitat in scientific palaeoecological publications some 15-20 years later.

Senior academic recollections

We approached a total of 95 senior academics, asking for their recollections of when they first heard the term mosaics applied to hominin environments, whether in Africa or in Asia (Table 3). These academics were chosen – after our literature search and discussions with a range of colleagues – as likely to have been at key conferences and other more informal meetings during the time when these ideas were starting to emerge. A total of 29 responded, and of these, eight respondents indicated that ecology books and books on human evolution had been highly influential, coupled with lectures at undergraduate level, and twelve said they were highly influenced by their own early fieldwork, or by discussions with colleagues who had done fieldwork in Africa. The balance of the respondents could not recall exactly the context in which the term appeared, but mentioned that by the time the term became current in publications, it had already been in use for some time at meetings and in conversation. One of these meetings may have been the IXth International Congress of Anthropological and Ethnological Sciences in Chicago, 1973, which will be discussed in more detail below.

The key point that came out of these responses was that the idea appears to have emerged slowly, rather than appearing as a new concept in any particular publication and that it is clear that it was being informally discussed in advance of its appearance in the formal literature. The response by the primatologist William (Bill) McGrew is typical: “My immediate response is that mosaic habitats just sort of crept in to the conversation.” In

addition most of the people suggested as key in early discussions and publications worked – or had been trained – in areas such as zoology, geography and forestry and only published on human evolution later in their careers.

Printed sources:

Our analysis of the published literature was based on extensive reading of paleoanthropological articles and books and those on related topics. In addition much of the scientific literature now exists in searchable digital archives, and this allows a more quantitative approach to tracking the spread of an idea – or to be more exact the terms (such as 'mosaic') associated with that idea (McIntosh, 1999). We have examined the first 40 years of the archive issues of the *Journal of Human Evolution* (1972-2011) to quantify the number of times in which the term 'mosaic' was used in reference to habitats (distinct from other uses such as 'mosaic evolution'[1], or 'photographic mosaic', which were disregarded). Of a total number of 3680 articles published over this 40 year span, only 88 make reference to mosaic habitats. The use of the term is becoming more common in recent years (Fig. 6), for the period 1972-1976, only three papers (i.e. less than 1%) of all papers published (n=473) used the term mosaic habitat, while for the later period 2007-2011, 37 articles of a

[1] Mayr (1982) records that the term 'mosaic evolution' was coined in 1954 by Gavin de Beer with reference to the genus *Archaeopteryx* (although the ideas had been around for many years before that) and it was being used in the palaeoanthropological literature by the late 1950s (e.g. Le Gros Clark, 1959b) in the context of a mix of 'advanced' and 'primitive' features in the same fossil. Thus, the use of 'mosaic evolution' predates the use of 'mosaic habitat' by some decades.

total of 652 articles mentioned this habitat type (almost 6%). This increasing trend is discernible for the case-study example for *Journal of Human Evolution*, but is also seen in several other publications listed in Table 2, reflecting the growth in detailed and specialised studies of palaeoenvironments of the last 40 years. Clearly the use of such quantitative analysis of key words in digital archives has drawbacks – a concept could be discussed but without the use of the focal key word. Because of this our extensive reading of the appropriate literature was especially important – both to spot use of the concept without the associated word 'mosaic' and to better understand the context in which mosaic was being used in any particular source.

Historic development of the mosaic concept

- *Years preceding the appearance of the mosaic – 1960's-1975*

In the years immediately preceding the widespread appearance of the mosaic habitat in print the conception of hominin habitats seems to have been a fairly simple dichotomy of early hominins moving from forest to open habitats (e.g. Sahni, 1952; Washburn and Howell, 1960; Schultz, 1961). The volume '*African Ecology and Human Evolution*' edited by Howell and Bouliére (1963) has a number of papers and discussion transcripts that discuss vegetation patchiness and a forest-grassland ecotone, although this latter term and the term mosaics was not used. By the end of the 1960s there was a clear shift in thinking, with people referring to the complexities of the savannah habitat. For example, John Napier (1967: 44) wrote "an environment neglected by scholars but one far better suited for the origin of man is the woodland-savanna,which is neither high forest nor open grassland". Glynn Isaac (1969: 8) was also well aware of the shortcomings of the open grassland version of the savannah model stating "Available data including the distribution of fossils make it

appear that savannah and open grassland was the ecological setting for early cultural developments, but African savannahs are extremely diverse in their biology, climate and physiography. We are wholly ignorant of the extent to which geographical or chronological variation amongst them or within them has influenced hominid evolution."

In this transitional period between the dominance of the classic savannah hypothesis and the arrival of the mosaic habitat, we have noted four key trends within the literature and the wider field: 1) a proliferation of primate studies, particularly in the wild; 2) the increase of large-scale African palaeoanthropological field projects with multiple specialists; 3) detailed research into the palaeoenvironments associated with Miocene localities (and fossils of primate genera like "*Ramapithecus*" *sensu lato*) such as Fort Ternan, Kenya (Tattersall, 1969; Andrews and Van Couvering, 1975; Andrews and Nesbit Evans, 1979; Shipman *et al*., 1981); and 4) an increase in interdisciplinary conferences and the publication of their proceedings, on specific topics such as chronology (Bishop and Miller, 1972), the Middle Pleistocene (Butzer and Isaac, 1975), and savannahs (Harris, 1980). Together, these four areas of specialization appear to have led to a deeper awareness of the role of ecology and African environments within palaeoanthropology, and they are reviewed below.

Primate studies. An increasing number of very detailed studies of African primate behaviour and ecology , on a range of taxa including vervets (*Chlorocebus pygerythrus)*, geladas (*Theropithecus gelada)*, baboons (*Papio* spp), and chimpanzees, (*Pan* spp.), provided the first detailed information about the ecology and behaviour of living primates (Goodall, 1965; Schaller, 1963; Reynolds and Reynolds, 1965; Rahm, 1967; Kortlandt, 1967; Struhsaker, 1967; Altmann and Altmann, 1970; Clutton-Brock, 1977). An important subset of these studies sought to link insights gleaned from primate behavioural studies to those of human evolution, and these were very influential in this respect (Washburn and DeVore, 1961; Jolly,

1970; Teleki, 1975; Washburn and McCown, 1978; Bernstein and Smith, 1979; Kortlandt, 1972; 1980a,b; Peters and O'Brien, 1981; Kinzey, 1987). Indeed Washburn and Howell (1960: 47) explicitly stated that "Extraordinarily little is known about the necessary background, including environmental situations and the particular structures, physiological mechanisms, or behaviour patterns, which formed the basis of the transition of some proto-hominid group to an early (australopithecine) grade. Certainly much more might be learned of these basic, important behavioural and structural preadaptations from field studies of African-ape behaviour in particular ecological situations."

As part of the focus on the free-living primate populations, there was necessary attention paid to the ecological aspects of their habitats, ranging behaviours and diets. Importantly, the emphasis widened from the gorillas and chimpanzees to examining other primate species as ecological models for hominins. Specifically, DeVore and Washburn (1963), DeVore and Hall (1965), and Hall and DeVore (1965) argued for the relevance of baboon ecology to the understanding of human evolution, because these terrestrial primates offered "some insights into the problems which confronted early man" (DeVore and Washburn, 1963:335). In addition during the late 1960s and early 1970's several biologists also argued that field studies of African social carnivores might be highly relevant to understanding hominin behaviour and ecology (e.g. Schaller and Lowther, 1969; Tinbergen, 1972).

Of the primate ecology studies, two stand out as being particularly important. Clifford Jolly's 1970 interpretation of seed-eating by geladas as model for early hominin diets and habitats seems to have been highly influential. Jolly envisioned the transition to seed-eating taking place "…in a dambo-like environment, later shifting to wider floodplains" (Jolly, 1970:21). Dutch ethologist, Adriaan Kortlandt, who wrote several papers on chimpanzees

and human evolution, was the author of the second influential study. He was the first to use the term 'mosaic habitat' in his 1972 book "*New perspectives on ape and human evolution"* which was obscurely published, but later reviewed across 22 pages of *Current Anthropology* in 1974, which may have helped bring the idea of the mosaics to a wider audience.

International field expeditions. Early field pioneers, such as Raymond Dart, Robert Broom, and Louis and Mary Leakey, tended to work alone or in small research groups, inviting specialists to become involved at appropriate stages in the research and publication. In the 1960s and early 1970s, a new model developed where large international and interdisciplinary field teams were put together and major field projects begun, such as the International Omo Research Expedition, the Koobi Fora Research Project, the Afar expedition and the Middle Awash Project (Boaz, 1981; Goodrum, 2013). These expeditions provided the opportunity for many young scientists to gain first-hand experience of the complexity of African habitats.

Detailed geological research led to a greater appreciation of the information inherent in the sedimentological contexts of hominin fossils (Bishop and Miller, 1972; Hay, 1976; Coppens *et al*., 1976; Bishop, 1978). These expeditions were also the impetus for the beginnings of some long-term actualistic research projects, such as those of Anna K. Behrensmeyer on taphonomy, in the Amboseli Basin (Kenya) and which have provided many new insights into African palaeoenvironments and site formation processes (e.g. Behrensmeyer, 1975; 1978; Western and Behrensmeyer, 2009).

Miocene site reconstructions. Analyses of primate-bearing deposits from the Siwaliks (Pakistan), Songor and Fort Ternan (Kenya) indicated that Miocene apes were most likely

associated with forest habitats. Therefore, at some point during the course of human evolution, a shift to terrestrial savannah habitats had occurred, to which Pat Shipman and colleagues (1981:49) ascribe the "appearance of *Ramapithecus* and other new species (that) may have been related to the ecological shift towards more open country". This habitat shift was considered a critical step in human evolution, which was linked to key hominin adaptations, such as the appearance of hunting behaviours (e.g. Cachel, 1976; Andrews and Nesbit Evans, 1979; Shipman *et al*., 1981). During this time, the term 'mosaic habitat' appeared in connection with the Siwalik palaeoenvironment, which was reconstructed as "a mosaic of more and less open habitats, rather than riparian forest" (Pilbeam *et al*., 1977:691). Andrews and Van Couvering (1975) used a detailed perspective of modern East African vegetation types, geology, geomorphology and faunas to reconstruct the Miocene faunal environments for sites such as Rusinga and Songor in Kenya. These authors described modern habitats as mosaics (in the ecological sense), but they did not apply this term to the Miocene palaeohabitats.

Conferences and conference proceedings. A number of major conferences took place in the early 1970s. Two were sponsored by the Wenner-Gren Foundation at Burg Wartenstein, Austria. The first was on dating of fossil sites in 1971 and the proceedings were published as *Calibration of Hominoid Evolution* (Bishop and Miller, 1972). The second was on the Middle Pleistocene in 1973 and published as *After the Australopithecines* (Butzer and Isaac, 1975). While the papers from the latter meeting were revised before publication, it is notable that three authors used the term mosaic in their chapters – Karl Butzer, Hilary Deacon and Glynn Isaac. In the concluding chapter Glynn Isaac also noted that during the conference both he and Hilary Deacon had been emphasizing the role of the "complex mosaics of biotopes in

Africa" acting as a buffer against climatic change (Isaac, 1975: 877). This meeting took place immediately before the 9th International Congress of Anthropological and Ethnological Sciences in Chicago and the results were reported there (Tax, 1975). The Chicago Congress was also attended by Adriaan Kortlandt who is recorded as using the term 'mosaic' in a discussion session (Anon, 1976) and by Susan Cachel who presented her paper on *Australopithecus* behaviour that explicitly used the word 'mosaic' (Cachel, 1976). Many of the senior figures in palaeoanthropology were present at the Chicago meeting, and it would appear, given the time lags that occur between writing papers and book publication, that these 1973 meetings may have been the catalyst for the rise of the term 'mosaic' from the mid-1970s onwards.

-*The mosaic spreads: 1976 onwards*

In Glynn Isaac's 1976 chapter in "*Human Origins: Louis Leakey and the East African Evidence*", published in California, he presented the evidence for hominin preferred habitats as follows:

> "In summary, the palaeoenvironmental reconstructions of the basins (i.e. Omo and Koobi Fora) that preserve Plio-Pleistocene archaeological traces suggest a mosaic of diverse habitats – beaches, reed beds, swamps, edaphic grassland, savanna, riverine woodland and bush, some gallery forest. …..I strongly suggest that it was the *diversity of resources* that may have been attractive. "
>
> (Isaac, 1976:501, original emphasis)

This chapter was republished verbatim two years later in the volume edited by Clifford Jolly (1978) entitled: "*Early hominids of Africa*" and published in London. It is possible that Isaac's

chapter enjoyed a wide readership on both sides of the Atlantic and that this visibility helped his proposition of the importance of the diversity offered by the mosaics of Africa gain wider acceptance. Harris and Isaac (1976) also mentioned mosaics in their reconstruction of the Karari escarpment (Kenya) palaeohabitat in the influential journal *Nature*.

High latitude studies of Pleistocene vegetation changes may also have played a role. Valerius Geist (1978: 214) emphasized the role of transitional areas in human evolution "The widely accepted notion…., that during the Miocene and Pliocene a drying trend forced arboreal apes to the ground to assume a terrestrial life on the savannah, is simply not tenable. It ignores the great opportunities of the forest-steppe [here steppe = savannah] ecotone". He also refers to the periglacial vegetation of northern latitudes as a mosaic (Geist, 1978: 202). Alan Gentry also cites high latitude Pleistocene vegetation changes as where he first met concepts of mosaic vegetation in his response to our e-mail survey.

By the late 1970's, several authors make use of the term in different contexts. In addition to the work in the Siwaliks (e.g. Pickford, 1977), authors such as Susan Cachel (1976:193) stated that "hominids lived in environmental mosaics, and not exclusively in a single, completely open-country environment" and Raymonde Bonnefille's palynological reconstructions of the lower Omo valley confirmed the "mosaic nature of the vegetation" (1976:428). In 1977, Karl Butzer placed hominins firmly within mosaics in a review paper that makes multiple reference to the importance of this habitat, and he states that "(t)he location of all early hominid sites (were) in mosaic environments along ecotones of the seasonally dry African 'savanna'" (Butzer, 1977:577). The mosaic had arrived in palaeoanthropology.

-The mosaic takes off: 1980 - present

In 1980, Adriaan Kortlandt published two papers on primate behaviour and habitats, with implications for human evolution, and both of these referred explicitly to the mosaic habitat (Kortlandt 1980a,b). J. Desmond Clark (1980) also mentioned both 'mosaic' and 'ecotone' in the first two pages of a chapter on the 'Early human occupation of African savanna environments' (part of a conference proceedings following a Wenner-Gren meeting on the topic of savannahs in 1978), demonstrating that both mosaics and ecotones were becoming established in discussions. Then, in 1981, two key papers were published; firstly, Bill McGrew and colleagues concluded that "vegetation of the East African Plio-Pleistocene was of a mosaic nature, a patchwork of riverine forest, open and closed woodland, scrub and dry and wet grassland" based on their chimpanzee studies in the dry savannah of Mount Assirik, Senegal (McGrew *et al*., 1981:241); secondly Owen Lovejoy's highly cited *Science* publication, entitled "*The origin of man*" linked omnivorous Miocene hominoids with "variable and mosaic conditions" (Lovejoy, 1981:344), and was probably instrumental in bringing the mosaic habitat term to the wider attention of palaeoanthropologists and students.

The present state of the mosaic habitat

Since then, the use of the mosaic has steadily increased in published articles, as shown in our summary of site reconstructions across Africa (Table 1) and our case study of the *Journal of Human Evolution* (Table 2 and Figure 6). However, there remains a lack of focus on the drivers of habitat heterogeneity as well as temporal and spatial scales. The challenge for the future will be to define and refine the temporal and spatial scale of the fossil mosaics, rather than simply noting that heterogeneous landscapes and vegetation were present at a site. There is now a desire on the part of palaeoecologists and palaeoanthropologists to focus on

the mosaic and clearly define its role in human evolution. The American Association of Physical Anthropology meeting in Calgary in 2014 hosted a themed session on mosaic habitats and the concept of scale emerged as being of central importance.

Conclusions

The term 'mosaic habitat' originated in plant ecology and started to be applied in palaeoanthropological thinking during the 1970's. The earliest usage we have found of 'mosaic' in specific reference to hominin habitats is by Adriaan Kortlandt (1972). Glynn Isaac related the term 'mosaic habitats' to the diversity of resources they offered to hominins (Isaac, 1976; 1978). From a history of science perspective this provides a good example of a concept that emerged over a period of time and became influential without ever becoming associated with one or two influential 'named' scientists. It also illustrates the importance of conferences and informal discussions – rather than just formal academic publication – in the development of scientific concepts.

The mosaic concept in terms of hominin landscapes and evolution remains loosely defined as a mixture of arboreal and savannah environments, typically around a water source at a fossil site. Defined in these general terms, it is easy to believe that these types of habitats are widespread, that they are stable and that they function in similar ways across regions. Importantly, this static view of mosaic habitats is at odds with what ecologists know about modern mosaics: that they are often a dynamic and unstable state in a vegetation succession between closed woodland and open grassland.

One of the problems with the present state of the mosaic concept is that it lacks a clear statement of what the appropriate temporal and spatial scales should be. Because a mosaic for a small mammal or insect is unlikely to be a mosaic for a hominin, scale is an important

missing part of the concept as a whole. We are in need of several, organism-specific definitions, instead of just a single definition. We may then be able to reassess the proper place of the Mosaic Habitat within the framework of human evolution studies.

Acknowledgements

We would like to thank numerous colleagues who shared their ideas, pictures, recollections and insights about the mosaic habitat concept, including Stanley Ambrose, Peter Andrews, René Bobe, Susan Cachel, John de Vos, Clive Gamble; Alan Gentry, Colin Groves, Ralph Holloway, Don Johanson, Clifford Jolly, Jonathan Kingdon, Owen Lovejoy, Bill McGrew, James Ohman, John Olsen, David Pilbeam, Peter Schmid, Jeanne Sept, Chris Stringer, Ian Tattersall, Francis Thackeray, Tim White, Edward O. Wilson, Milford Wolpoff, and Richard Wrangham. Goran Strkalj made useful comments on an earlier version of this manuscript. We would like to thank the Editor Margaret Avery and two anonymous referees for their comments which have improved this manuscript. This work is part of the *Quantifying the Mosaic* project, funded by the Leverhulme Trust (grant number RPG-2012-472) and we thank them for their support.

References

ALTMANN, S.A. & ALTMANN, J. 1970. *Baboon ecology*. Chicago, University of Chicago Press.

ANDREWS, P. & VAN COUVERING, J.A.H. 1975. Palaeoenvironments in the East African Miocene. In, Szalay, F.S. (Ed.) *Approaches to Primate Paleobiology*. Basel, Karger. pp. 62-103.

ANDREWS, P. & NESBIT EVANS, E. 1979. The environment of *Ramapithecus* in Africa.

Palaeobiology 5: 22-30.

ANDREWS, P. & STRINGER, C. 1989. *Human evolution, an illustrated guide*. British Museum (Natural History), London.

ANDREWS, P. & BAMFORD, M. 2008. Past and present vegetation ecology of Laetoli, Tanzania. *Journal of Human Evolution* 54: 78-98.

ANON. 1976. Discussion. In Tuttle, R.H. (Ed.) *World Anthropology: Primate functional morphology and evolution*. Stuttgart, Walter de Gruyter. pp. 229.

BAMFORD, M.K. 1999. Pliocene fossil woods from an early hominid cave deposit, Sterkfontein, South Africa. *South African Journal of Science* 95: 231-237.

BEHRENSMEYER, A.K. 1975. The Taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology, Harvard*. 146: 473-578.

BEHRENSMEYER, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150-162.

BELSKY, A.J. 1986. Population and community processes in a mosaic grassland in the Serengeti, Tanzania. *Journal of Ecology* 74: 841-856.

BENDER, R., TOBIAS, P.V. & BENDER, N. 2012. The Savannah Hypotheses: origin, reception and impact on paleoanthropology. *History and Philosophy of the Life Sciences* 34: 147–184.

BERNSTEIN, I. 1967. Defining the natural habitat. In Starck, D., Schneider,R., Kuhn, H.-J. (Eds.) *Progress in primatology*. Stuttgart: Gustav Fischer Verlag. pp 177-179.

BERNSTEIN, I.S. & SMITH, E.O. (Eds.) 1979. *Primate ecology and human origins: Ecological influences on social organization.* Garland STPM Press: New York and London.

BLUMENSCHINE, R.J., STANISTREET, I.G., NJAU, J.K., BAMFORD, M.K., MASAO, F.T., ALBERT, R.M., STOLLHOFEN, H., ANDREWS, P., PRASSACK, K.A., MCHENRY, L.J., FERNÁNDEZ-JALVO, Y., CAMILLI, E.L. & EBERT, J.I. 2012. Environments and hominin activities across the FLK Peninsula during *Zinjanthropus* times (1.84 Ma), Olduvai Gorge, Tanzania. *Journal of Human Evolution* 63: 364-383.

BISHOP, W.W. & MILLER, J.A. (Eds.) 1972. *Calibration of Hominoid Evolution*. The Wenner-Gren Foundation for Anthropological Research, New York. Scottish Academic Press; University of Toronto Press.

BISHOP, W.W. (Ed.) 1978. Geological background to fossil man: Recent research into the Gregory Rift Valley, East Africa. *Geological Society of London, Special publications* 6: 1-4.

BOAZ, N.T. 1981. History of American paleoanthropological research on early Hominidae, 1925-1980. *American Journal of Physical Anthropology* 56: 397-405.

BOBE, R., ECK, G.G. 2001. Responses of African bovids to Pliocene climatic change. *Paleobiology Memoirs* 27: 1-48.

BOBE, R. 2006. The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments* 66: 564-584.

BOND, W.J. & KEELEY, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387-394.

BONNEFILLE, R. 1976. Palynological evidence for an important change in the vegetation of the Omo Basin between 2.5 – 2 million years ago. In Coppens, Y., Howell, F.C., Isaac, G.Ll. & Leakey, R.E.F. (Eds.) *Earliest man and environments in the Lake Rudolf Basin*. Chicago, University of Chicago Press. pp. 421-431.

BOWLER, P.J. 1986. *Theories of human evolution. A century of debate 1844-1944*. Baltimore, John Hopkins University Press.

BOWLER, P.J. 2003. *Evolution; the history of an idea*. 3rd ed. Berkeley, University of California Press.

BRUNET, M., BEAUVILAIN, A., COPPENS, Y., HEINTZ, E., MOUTAYE, A.H.E. & PILBEAM, D. 1995. The first australopithecine 2500 kilometres west of the Rift Valley (Chad). *Nature* 378: 273-275.

BUTZER, K.W. 1971. *Environment and archaeology; an environmental approach to prehistory*. 2nd ed. London, Methuen and Co.

BUTZER, K.W. 1977. Environment, culture and human evolution. *American Scientist* 65: 572-584.

BUTZER, K.W. and ISAAC, G.Ll. (eds). 1975. *After the Australopithecines: Stratigraphy, ecology, and culture change in the Middle Pleistocene*. The Hague: Mouton.

CACHEL, S. 1976. A new view of speciation in *Australopithecus*. In Tuttle, R.H. (Ed.) *Paleoanthropology, Morphology and Paleoecology*. Paris, Mouton. pp. 183-201.

CALOW, P. 1999. *Blackwell's concise encyclopaedia of ecology*. Oxford, Blackwell Science.

CAMPBELL, B.G. 1967. *Human Evolution, an introduction to man's adaptations*. London, Heinemann Educational Books.

CAMPBELL, B.G. 1974. *Human Evolution, an introduction to man's adaptations* (2nd edition). London, Heinemann Educational Books.

CAMPIONI, L., HERNÁN SARASOLA, J., SANTILLÁN, M., & MATÍAS REYES, M. 2013. Breeding season habitat selection by ferruginous pygmy owls *Glaucidium brasilianum* in central Argentina. *Bird Study* 60: 35-43.

CARTMILL, M., PILBEAM, D. & ISAAC, G. 1986. One hundred years of paleoanthropology.

American Scientist 74: 410-420.

CAVERS, F. 1914. Gola's osmotic theory of Edaphism. *Journal of Ecology* 2: 209-231.

CLARK, J.D. (Ed.) 1957. *Third Pan-African Congress on Prehistory, Livingstone, 1955*. London, Chatto and Windus.

CLARK, J.D. 1980. Early human occupation of African savanna environments. In Harris, D.R. (ed.) *Human ecology in savanna environments*. London, Academic Press. pp. 41-71.

CLARK, J.D., BEYENE, Y., WOLDEGABRIEL, G., HART, W.K., RENNE, P.R., GILBERT, H., DEFLEUR, A., SUWA, G., KATOH, S., LUDWIG, K.R., BOISSERIE, J-R., ASFAW, B. & WHITE, T.D. 2003. Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 747-752.

CLUTTON-BROCK, T.H. (Ed.) 1977. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, Academic Press.

COOKE, H.B.S. 1978. Faunal evidence for the biotic setting of Early African hominids. In Jolly, C. (Ed.) *Early hominids of Africa*. London, Gerald Duckworth and Co. pp. 267-281.

COPPENS, Y., HOWELL, F.C., ISAAC, G.LL. & LEAKEY, R.E.F. (Eds.) 1976. *Earliest man and environments in the Lake Rudolf Basin*. Chicago, University of Chicago Press.

DART, R.A. 1925. *Australopithecus africanus. Nature* 115: 195–199.

DARWIN, C. 1871. *The descent of man, and selection in relation to sex.* London, John Murray.

DE LA TORRE, I. 2011. The origins of stone tool technology in Africa: a historical perspective. *Philosophical Transactions of the Royal Society B*. 366: 1028-1037.

DeMENOCAL, P.B. 1995. Plio-Pleistocene African climate. *Science* 270: 53-59.

DeMENOCAL, P.B. 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220: 3-24.

DeMENOCAL, P.B. 2011. Climate and human evolution. *Science* 331: 540-542.

DeVORE, I. & Hall, K.R.L. 1965. Baboon ecology. In DeVore, I. (Ed.) *Primate behaviour: Field studies of monkeys and apes*. New York, Holt Rinehart and Winston. pp. 20-52.

DeVORE, I. & WASHBURN, S.L. 1963. Baboon ecology and human evolution. In Clark Howell, F. & Bourlière, F. (Ed.) *African ecology and human evolution.* Chicago, Aldine Publishing Company. pp. 335-367.

DOMÍNGUEZ-RODRIGO, M. 2014. Is the "Savanna Hypothesis" a dead concept for explaining the emergence of the earliest hominins? *Current Anthropology* 55: 59-81.

EDEY, M.A. 1973. *The Missing Link*. Time Life International (Nederland) B.V.

ELLIOT SMITH, G. 1924. *The evolution of man: essays*. London, H. Milford, Oxford University Press.

ELTON, S. 2008. The environmental context of human evolutionary history in Eurasia and Africa. *Journal of Anatomy* 12: 377–393.

FIEBEL, C.S. 2011. A geological history of the Turkana Basin. *Evolutionary Anthropology* 20: 206-216.

FINLAYSON, C. 2009. *The humans who went extinct: why Neanderthals died out and we survived*. Oxford, Oxford University Press.

FINLAYSON, C., CARRIÓN, J., BROWN, K., FINLAYSON, G., SÁNCHEZ-MARCO, A., FA, D., RODRÍGUEZ-VIDAL, J., FERNÁNDEZ, S., FIERRO, E., BERNAL-GÓMEZ, M. & GILES-PACHECO, F. 2011. The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quaternary Science Reviews* 30: 1525-1532.

FONDERFLICK, J., BESNARD, A. & MARTIN, J-L. 2013. Species traits and the response of open-habitat species to forest edge in landscape mosaics. *Oikos* 122: 42-51.

GEIST, V. 1978. *Life strategies, human evolution, environmental design: toward a biological theory of health*. New York, Springer-Verlag.

GLEN, W. (Ed.) 1994. *The mass-extinction debates: how science works in a crisis*. Stanford University Press, Stanford.

GOODALL, J. 1965. Chimpanzees of the Gombe Stream Reserve. In DeVore I. (Ed.) *Primate behaviour: Field studies of monkeys and apes*. New York, Holt Rinehart and Winston, pp. 425-473.

GOODRUM, M.R. 2013. History. In Begun, D.R. (Ed.) *A companion to Paleoanthropology*. Chichester, Wiley-Blackwell. pp. 17-33.

GOULD, S.J. 2002. The structure of evolutionary theory. Cambridge, Mass., Harvard University Press.

HAILE-SELASSIE, Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412: 178-181.

HALL, K.R.L. & DEVORE, I. 1965. Baboon social behavior. In DeVore I. (Ed.) *Primate behaviour: Field studies of monkeys and apes*. New York, Holt Rinehart and Winston. pp. 53-110.

HARRIS, D.R. (Ed.) 1980. *Human ecology in savanna environments*. London, Academic Press.

HARRIS, J.W.K. & ISAAC, G. 1976. The Karari Industry: early Pleistocene archaeological evidence from the terrain east of Lake Turkana, Kenya. *Nature* 262: 102-107.

HAY, R.L. 1976. *Geology of the Olduvai Gorge: A Study of Sedimentation in a Semiarid Basin*. Berkeley, University of California Press.

HOPLEY, P.J., LATHAM, A.G. & MARSHALL, J.D. 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: A stable

isotope and dental microwear approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 233: 235-251.

HOWELL, F.C. & BOULIÈRE, F. 1963. *African Ecology and Human Evolution*. Chicago, Aldine Publishing Company.

HOWELL, F.C. 1970. *Early man* (2nd edition). New York, Time Life Books.

HUTCHINSON, G.E. 1965. *The ecological theater and the evolutionary play*. New Haven and London, Yale University Press.

ILN, 2013. Heritage. http://www.iln.co.uk/heritage/ [accessed 11/06/2013]

ISAAC, G.Ll. 1969. Studies of early culture in East Africa. *World Archaeology* 1: 1-28.

ISAAC, G.Ll. 1975. Sorting out the Muddle in the Middle: an Anthropologist's post-conference appraisal. In Butzer, K.W. & Isaac, G.Ll. (Eds.) *After the Australopithecines: Stratigraphy, ecology, and culture change in the Middle Pleistocene*. The Hague: Mouton. pp. 875-887.

ISAAC, G.Ll. 1976. The activities of early African hominids: a review of archaeological evidence from the time span two and a half to one million years ago. In Isaac, G.L. & McCOWN, E. (Eds.) *Human Origins: Louis Leakey and the East African Evidence*. Menlo Park, California, W.A. Benjamin, Inc. pp. 483-514.

ISAAC, G.Ll. 1978. The archaeological evidence for the activities of early African hominids. In JOLLY, C. J. (Ed.) *Early hominids of Africa*. London, Duckworth. pp. 219-254.

JOLLY, C.J. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5: 5-26.

JOLLY, C.J. 1978. *Early hominids in Africa.* London, Duckworth.

KEITH, A. 1925. *The antiquity of man*. 2nd ed. London, Williams and Northgate.

KENT, M. 2011. *Vegetation description and data analysis*. 2nd ed. Chichester, Wiley-Blackwell.

KINGSTON, J.D. 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Yearbook of Physical Anthropology* 50: 20-58.

KINGSTON, J.D., DEINO, A.L., EDGAR, R.K. & HILL, A. 2007. Astronomically forced climate change in the Kenyan Rift Valley 2.7-2.55 Ma: implications for the evolution of early hominin ecosystems. *Journal of Human Evolution* 53: 487-503.

KINGSTON, J.D. & HARRISON, T. 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeography Palaeoclimatology Palaeoecology* 243: 272-306.

KINZEY, W.G. (Ed.). 1987. *The evolution of human behaviour: primate models*. Albany: State University of New York Press.

KORTLANDT, A. 1967. Experimentation with chimpanzees in the wild. In Starck, D., Schneider, R. & Kuhn, H-J. (Eds.) *Progress in primatology*. Stuttgart, Gustav Fischer Verlag. pp 209-224.

KORTLANDT, A. 1972. *New perspectives on ape and human evolution*. Amsterdam, Stichting voor psychobiologie.

KORTLANDT, A. 1980a. How might early hominids have defended themselves against large predators and food competitors? *Journal of Human Evolution* 9: 79-112.

KORTLANDT, A. 1980b. The Fayum primate forest: did it exist? *Journal of Human Evolution* 9: 277-297.

KUMAN, K., CLARKE, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein Member 5. *Journal of Human Evolution* 38: 827-847

LE GROS CLARK, W.E. 1959a. *The antecedents of man*. New York, Quadrangle/The New York Times Book Co. 3rd edition.

LE GROS CLARK, W.E. 1959b. Penrose Memorial Lecture: the crucial evidence for human evolution. *Proceedings of the American Philosophical Society* 103: 159-172.

LE GROS CLARK, W.E. 1967. *Man-apes or Ape-Men? The stories of discovery in Africa*. New York, Holt Rinehart and Winston, Inc.

LAMARCK, J.B. 1809. *Philosophie zoologique*. Paris, Dentu.

LEAKEY, L.S.B. 1957. Preliminary report on a Chellean 1 living site at BK II, Olduvai. In Clark, J.D., Cole, S. (Eds.) *Proceedings of the 3rd Pan-African Congress on Prehistory*. London, Chatto and Windus. pp. 217–218.

LEAKEY, L.S.B. 1958. Recent discoveries at Olduvai Gorge, Tanganyika. *Nature* 181: 1099-1103.

LEAKEY, L.S.B. 1960. The origins of the genus *Homo*. In Tax, S. (Ed.) *The evolution of man: man, culture and society. Volume 2 of evolution after Darwin*. Chicago, University of Chicago Press. pp. 17-32.

LEAKEY, L.S.B. 1965. *Olduvai Gorge 1951-61. Volume 1*. Cambridge, Cambridge University Press.

LEAKEY, L.S.B. & GOODALL, V.M. 1970. *Unveiling man's origins*. London, Methuen & Co.

LEAKEY, M.G., SPOOR, F., BROWN, F.H., GATHOGO, P.N., KIARIE, C., LEAKEY, L.N. & MCDOUGALL I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410: 433-440.

LOVEJOY, C.O. 1981. The origin of man. *Science* 211: 341-350.

MARIMON, B.S., MARIMON-JUNIOR, B.H., FELDPAUSCH, T.R., OLIVEIRA-SANTOS, C., MEWS, H.A., LOPEZ-GONZALES, G., LLOYD, J., FRANCZAK, D.D., DE OLIVERIRA, E.A.,

MARACAHIPES, L., MIGUEL, A., LENZA, E. & PHILLIPS, O.L. 2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. *Plant Ecology and Diversity* 7: 281-292.

MAYR, E. 1980. Some thoughts on the history of the evolutionary synthesis. In Mayr, E. & Provine, W.B. (Eds.) *The evolutionary synthesis*. Cambridge Mass., Harvard University Press. pp 1-48.

MAYR, E. 1982. *The growth of biological thought – diversity, evolution, inheritance*. Cambridge Mass., Belknap, Harvard.

MCGREW, W.C., BALDWIN, P.J. & TUTIN, C.E.G. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution* 10: 227-244.

MCINTOSH, R.P. 1999. The succession of succession: a lexical chronology. *Bulletin of the Ecological Society of America* 80: 256-265.

MEDAWAR, P. 1963. Is the scientific paper a fraud? Reprinted in Medawar, P. 1990. *The threat and the glory*. Oxford, Oxford University Press.

MICHELMORE, A.P.G. 1934. Letter to the editor: vegetation succession and regional surveys, with special reference to tropical Africa. *Journal of Ecology* 22: 313-317.

MICHELMORE, A.P.G. 1939. Observations on tropical African grasslands. *Journal of Ecology* 27: 282-312.

MILNER, R. 2012. *Charles R Knight; the artist who saw through time*. New York, Abrams.

NAPIER, J. 1967. The antiquity of human walking. Scientific American. Reprinted in Katz, S.H. (1975) *Biological anthropology, readings from Scientific American*. San Francisco, W.H. Freeman and Company. pp. 36-46.

NEE, S. 2007. Metapopulations and their spatial dynamics. In May, R.M. & McLean, A.R. (Eds.) *Theoretical ecology* 3rd ed. Oxford Oxford University Press. pp 35-45.

PETERS, C.R. 1979. Toward an ecological model of African Plio-Pleistocene hominid adaptations. *American Anthropologist* 81: 261-278.

PETERS, C.R. & O'BRIEN, E.M. 1981. The early hominid plant-food niche: insights from an analysis of plant exploitation by *Homo*, *Pan*, and *Papio* in eastern and southern Africa. *Current Anthropology* 22: 127-140.

PICKFORD, M. 1977. Pre-human fossils from Pakistan. *New Scientist* September 8th: 578-580.

PILBEAM, D., MEYER, G.E., BADGLEY, C., ROSE, M.D., PICKFORD, M.H.L., BEHRENSMEYER, A.K. & SHAH, S.M.I. 1977. New hominoid primates from the Siwaliks of Pakistan and their bearing on hominoid evolution. *Nature* 270: 689-695.

POTTS R. 1998. Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology* 41: 93-136.

POTTS, R. 2013. Hominin evolution in settings of strong environmental variability. *Quaternary Science Reviews* 73: 1-13.

POUND, R. & CLEMENTS, F.E. 1897. Observations on the distribution of plants along the shore at Lake of the Woods. American Naturalist 31: 980-984.

PRIVATEER, P. 2005. Romancing the human: the ideology of envisioned human origins. In Smiles, S. & Moser, S. (Eds.) *Envisioning the past*. Oxford, Blackwell. pp 1-28.

RAHM, U. 1967. Observations during chimpanzee captures in the Congo. In Starck, D. Schneider, R. & Kuhn, H-J. (Eds.) *Progress in primatology*. Stuttgart, Gustav Fischer Verlag. pp 195-207.

REED, K.E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene *Journal of Human Evolution* 32: 289–322.

REED, K.E. 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. *Journal of Human Evolution* 54: 743-768.

REED, K.E. 2013. Multiproxy paleoecology: reconstructing evolutionary context in paleoanthropology. In Begun, D. R., (ed) *A companion to Paleoanthropology*, Chichester: Wiley-Blackwell. pp 204-225.

RETALLACK, G.J. 2001. *Soils of the past; an introduction to Paleopedology*. Oxford, Blackwell Science.

REYNOLDS, V. & REYNOLDS, F. 1965. Chimpanzees of the Budongo Forest. In DeVore, I. (Ed.) *Primate behaviour: Field studies of monkeys and apes*. New York, Holt Rinehart and Winston. pp. 368-424.

REYNOLDS, S.C., BAILEY, G. & KING, G.C.P. 2011. Landscapes and their relation to hominin habitats: case studies from *Australopithecus* sites in eastern and southern Africa. *Journal of Human Evolution* 60: 281-298.

RUDWICK M. 1976. The emergence of a visual language for geological science, 1760-1840. *History of Science* 14: 149-206.

SAHNI, M.R. 1952. *Man in evolution*. Calcutta, Orient Longmans Ltd.

SAPP, J. 2009. *The new foundations of evolution*. Oxford, Oxford University Press.

SCHALLER, G.B. 1963. *The Mountain Gorilla; ecology and behaviour*. Chicago, University of Chicago Press.

SCHALLER, G.B., LOWTHER, G.R. 1969. The relevance of carnivore behaviour in the study of early hominins. *Southwestern Journal of Anthropology* 27: 30-45.

SCHOENINGER, M.J., REESER, H. & HALLIN, K. 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. Journal of Anthropological Archaeology 22: 200-207.

SCHULTZ, A.H. 1961. Some factors influencing the social life of primates in general and of early man in particular. In Washburn, S. (Ed.) *Social life of early man*. London, Methuen & Co, Ltd. pp. 58-90

SHIPMAN, P., WALKER, A., VAN COUVERING, J.A., HOOKER, P.J. & MILLER, J.A. 1981. The Fort Ternan hominoid site, Kenya: geology, age, taphonomy and paleoecology. *Journal of Human Evolution* 10:49-72.

SHORROCKS, B. 2007. *The biology of African Savannahs*. Oxford: Oxford University Press.

SINCLAIR, A.R.E. 2012. *Serengeti story: life and science in the world's greatest wildlife region*. Oxford, Oxford University Press.

SINGER, R. 1957. Investigations at the Hopefield site. In Clark, J.D. (Ed.). *Third Pan-African Congress on Prehistory, Livingstone, 1955*. London, Chatto & Windus. pp. 175-182.

SOININEN, E.M., BRÅTHEN, K.A., JUSDADO, J.G.H., REIDINGER, S. & HARTLEY, S.E. 2013. More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. *Oikos* 122: 30-41.

SPONHEIMER, M. & LEE-THORP, J.A. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283: 368-370.

STRINGER, C. & ANDREWS, P. 2005. *The complete world of human evolution*. London, Thames & Hudson.

STRUHSAKER, T.T. 1967. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli game reserve, Kenya. *Ecology* 48: 891-904.

TATTERSALL, I. 1969. Ecology of the North Indian *Ramapithecus*. *Nature* 221: 451-542.

TATTERSALL, I. 2000. Paleoanthropology: the last half-century. *Evolutionary Anthropology* 9: 2-16.

TAX, S. 1975. General Editor's preface. In Butzer, K.W. & Isaac G.Ll. (Eds.) *After the*

Australopithecines: Stratigraphy, ecology, and culture change in the Middle Pleistocene. The Hague: Mouton. pp. v.

TELEKI, G. 1975. Primate subsistence patterns: collector-predators and gatherer-hunters. *Journal of Human Evolution* 4: 125-184.

TINBERGEN, N. 1972. Forward. In Kruuk, H. *The spotted hyena*. Chicago, Chicago University Press.

TORELLO-RAVENTOS, M., FELDPAUSCH, T.R., VEENENDAAL, E., SCHRODT, F., SAIZ, G., DOMINGUES, T.F., DJAGBLETEY, G., FORD, A., KEMP, J., MARIMON, B.S., MARIMON JR, B.H., LENZA, E., RATTER, J.A., MARACAHIPES, L., QUESADA, C.A., ISHIDA, F.Y., NARDOTO, G.B., AFFUM-BAFFOE, K., ARROYO, L., BOWMAN, D.M.J.S., COMPAORE, H., DAVIES, K., DIALLO, A., FYLLAS, N.M., GILPIN, M., HEIN, F., JOHNSON, M., KILLEEN, T.J., METCALFE, D., MIRANDA, H.S., STEININGER, M., THOMSON, J., SYKORA, K., MOUGIN, E., HIERAUX, P., BIRD, M.I., GRACE, J., LEWIS, S.L., PHILLIPS, O.L. & LLOYD, J. 2013. On the delineation of tropical vegetation types with an emphasis on forest/savannah transitions. *Plant ecology and diversity* 6: 101-137.

TRAUTH, M.H., MASLIN, M.A., DEINO, A.L., JUNGINGER, A., LESOLOYIA, M., ODADA, E.O., OLAGO, D.O., OLAKA, L.A., STRECKER, M.R. & TEIDEMANN, R. 2010. Human evolution in a variable environment: the amplifier lakes of Eastern Africa. *Quaternary Science Reviews* 29: 2981-2988.

VESEY-FITZGERALD, D.F. 1963. Central African grasslands. *Journal of Ecology* 51: 243-274.

VIGNAUD, P., DURINGER, P., MACKAYE, H.T., LIKIUS, A., BLONDEL, C., BOISSERRIE, J-R., DE BONIS, L., EISENMANN, V., ETIENNE, M.E., GERAADS, D., GUY, F., LEHMANN, T., LIHOREAU, F., LOPEZ-MARTINEZ, N., MOURER-CHAVIRÉ, C., OTERO, O., RAGE, J-C.,

SCHUSTER, M., VIRIOT, L., ZAZZO, A. & BRUNET, M. 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418: 152-155.

VRBA, E.S. 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. *Nature* 250: 19-23.

VRBA, E.S. 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* 254: 301–304.

VRBA, E.S. 1980. Evolution, species and fossils: how does life evolve? South African Journal of *Science* 76: 61-84.

WASHBURN, S.L. & HOWELL, F.C. 1960. Human evolution and culture. In Tax, S. (Ed.) *The evolution of Man: Man, culture and society, volume 2 of evolution after Darwin*. Chicago, University of Chicago Press. pp. 33-56

WASHBURN, S.L. & DEVORE, I. 1961. Social behavior of baboons and early man. In Washburn, S.L. (Ed.). *The Social life of early man*. New York, Viking Fund. pp 91-105.

WASHBURN, S.L. & MCCOWN, E.R. (Eds.) 1978. *Human Evolution: Biosocial perspectives. Perspectives on human evolution, Volume IV*. Society for the study of human evolution inc, Berkley, California, The Benjamin/Cummings publishing company.

WATT, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1-22

WELLS, H.G., HUXLEY, J.S., WELLS, G.P. 1931. *The science of life vol 3.* London, Waverley Book Company.

WELLS, L.H. & COOKE, H.B.S. 1956. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrus. *Palaeontologia Africana* 4: 1-55.

WESTERN, D. & BEHRENSMEYER, A.K. 2009. Bone assemblages track animal community structure over 40 years in an African savanna ecosystem. *Science* 324: 1061-1064.

WHITE, T.D., SUWA, G., HART, W.K., WALTER, R.C., WOLDEGABRIEL, G., DE HEINZELIN, J., CLARK, J.D., ASFAW, B., VRBA, E. 1993. New discoveries of *Australopithecus* at Maka, Ethiopia. *Nature* 366: 261-265.

WHITE, T.D., ASFAW, B., DEGUSTA, D., GILBERT, H., RICHARDS, G.D., SUWA, G., HOWELL, F.C. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 742-747.

WILSON, E.O. 1975. *Sociobiology; the new synthesis*. Cambridge, Mass., Harvard University Press.

WILSON, E.O. 2012. *The social conquest of Earth*. Liveright Publishing, New York.

WOLDEGABRIEL, G., HAILE-SELASSIE, Y., RENNE, P.R., HART, W.K., AMBROSE, S.H., ASFAW, B., HEIKEN, G., WHITE, T. 2001. Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. *Nature* 412: 175-177.

WOOD, B. & STRAIT, D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* 46: 119-162.

WYNN, J.G., ALEMSEGED, Z., BOBE, R., GERAADS, D., REED, D. & ROMAN, D.C. 2006. Geological and palaeontological context of a Pliocene juvenile hominin at Dikika, Ethiopia. *Nature* 443: 332-336.

Figure captions:

Figure 1:

Examples of South African savannahs in the Kruger National Park. Savannah is loosely defined as a highly variable mix of grass and trees (Shorrocks, 2007): left, a 'classic' open savannah of the sort envisaged in relation to Dart's savannah hypothesis; right, a mosaic of open and more wooded patches.

Figure 2:

A reconstruction of *Australopithecus africanus* by Amédée Forestier published on February 14th 1925 on the front page of the *Illustrated London News*, a pictorial newspaper published in the UK from 1842-2003 (ILN, 2013). This vignette shows an emphasis on the head, and no detail about the postcrania and habitats of early hominins, in keeping with the state of knowledge at that time.

Figure 3:

A full length reconstruction of *Australopithecus africanus* also published on February 14th 1925 on the inside pages of the *Illustrated London News*. The caption reads "links in the chain of human evolution: *Australopithecus* (3 ft. high, on the left), representing the Taungs skulls, and his later compatriot, the "Rhodesian" (6 ft.)m representing the Broken Hill skull." Despite only skulls being available, the complete hominins have been reconstructed by Forestier under the direction of Professor G. Elliot Smith. Note the emphasis is on the hominins, with a very generalised background.

Figure 4:

By 1951, some paleoenvironmental detail appears in this reconstruction of *Australopithecus africanus* in South Africa (by Maurice Wilson, published in the *Illustrated London News* on December 8th 1951). The accompanying text reads "They frequented caves in dry, open country, and may have been partly carnivorous." Mary Evans / Natural History Museum.

Figure 5:

An illustration of 'Chellean' hominins at Olduvai Gorge, published in the *Illustrated London News* on June 28th 1958. The reconstruction is by Neave Parker, following guidance from L.S.B. Leakey, and the accompanying text states "The illustration above shows Chellean hunters on their campsite near a shallow marshy stream." © Illustrated London News Ltd/Mary Evans.

Figure 6:

Review of the archive issues of the *Journal of Human Evolution* since its inception in 1972 indicates a steady rise in the use of the term 'mosaic habitat'. The data were calculated as follows: each mention of mosaic habitat was recorded (each article was only counted once) and the total number of articles published (n=3680) were summed into five year bins and expressed as a percentage.

Table 1:

Country and site	Reconstruction	Data type and references
Chad: Toros-Menalla	"a mosaic of environments from gallery forest at the edge of a lake area to a dominance of large savannah and grassland"	Macromammalian taxa (Vignaud *et al*., 2002: 155).
Chad: Koro Toro	"a lakeside environment, with both perennial and permanent streams, and a vegetational mosaic of gallery forest and wooded savannah with open grassy patches."	Macromammalian taxa (Brunet *et al*., 1995: 273).
Ethiopia: Middle Awash, (Sangatole and Asa Koma Members)	"Predominantly wet and closed woodland/forest" combined with "wooded grasslands around lake margins"	Macro-, micromammalian taxa (WoldeGabriel *et al*., 2001: 177), (Haile-Selassie, 2001).
Ethiopia: Middle Awash, (Maka)	"Ecologically intermediate between the contemporary open, dry Laetoli environment and the more closed, mesic Hadar SH member environment"	Macro-, micromammalian taxa (White *et al*., 1993: 263).
Ethiopia: Middle Awash, (Bouri Formation, Upper Herto Member)	"Proximity of both aquatic and grassland habitats" and "margin of freshwater lake"	Macro-, micromammalian taxa (White et al., 2003), (Clark *et al*., 2003: 750, 751).
Ethiopia: Hadar (12 submembers of Hadar and Busidima formations)	"intermediate cover habitats of bushland, open woodland, and shrubland with varying regions of wetlands or edaphic grasslands through time"	Macromammalian taxa (Reed, 2008: 763).
Ethiopia: Dikika	"a mosaic of mesic habitats"	Faunal evidence

		(Wynn *et al*., 2006:335).
Kenya: Allia Bay, East Turkana	"overall mosaic of environments"	Herbivore enamel stable isotopes (Schoeninger *et al*., 2003:200).
Kenya, Turkana basin	"mosaic of habitats and associated communities"	Sediments, (Fiebel, 2011: 210).
Kenya, Lomekwi	"a mosaic of habitats, but with predominantly woodland and forest-edge species dominating"	Faunal evidence (Leakey *et al*., 2001: 439).
Tanzania: Olduvai (FLK peninsula)	"Good drainage on the Peninsula permitted the establishment of trees. Short grass/ sedgeland occurred in open areas on the Peninsula and in the Channel, while the Wetland was a mixed-species marshland with areas of open water."	Landscape and faunal evidence (Blumenschine *et al*., 2012: 381).
Tanzania: Laetoli	"a mosaic of low and tall deciduous woodlands and with riverine woodland and forest associations along water courses." (a) and also: "heterogeneous ecosystems with both C_3 and C_4 dietary plants available that could support grassland, woodland, and forested communities". (b)	a) Vegetation (Andrews and Bamford, 2008: 78). b) Herbivore enamel stable isotopes (Kingston and Harrison, 2007: 272)
South Africa: Sterkfontein (Member 4 and later)	"overall change from tropical to sub-tropical gallery forest, forest fringe and woodland conditions in Member 4 to more open woodland and grassland habitats in the later units" (b), based partly on (c)	a) Fossil wood (Bamford, 1999); b) Macromammalian fossils (Kuman and Clarke, 2000: 827); c) Vrba, 1974, 1975
South Africa:	"a mosaic of grassland and tree cover	Stable isotopes of

Swartkrans	which was probably denser alongside the ancient Blaaubank stream"	mammalian enamel (Sponheimer and Lee-Thorp, 1999: 724).
South Africa: Makapansgat	"a woodland–savannah mosaic with a greater proportion of woodland than savannah"	Multiproxy analysis of microwear and stable isotopes (Hopley *et al*., 2006:248).

Table 1: A sample of hominin habitat reconstructions from sites in Chad, Ethiopia, Kenya, Tanzania and South Africa. Additional reconstructions given in Wood and Strait (2004:134-136), and Reed (2013). In most cases, the term 'mosaic' signals a variety or diversity of habitat and vegetation types.

Table 2:

Source	Information
Digital archives: *Journal of Human Evolution* (1972-2011, quantified in Fig. 5) *Current Anthropology* (1959-2012) *Man* (1901-1994) *Science* (1880-2012) *Nature* (1950-2012) *Scientific American* (1845-2012) *Sigma-Xi Quarterly;* followed by *American Scientist* (1913-2007) *American Anthropologist* (1888-2005)	Search for specific terms gives indication of years in which terms feature in published articles. Determines a likely period in which term becomes more widely used in scientific literature. Frequently cited papers indicate key texts. Citation data from Web of Science taken as an indicator of the influence of these publications.
E-mail survey: Sent to 90+ senior academics, artists involved in hominin reconstructions and 'popular', science authors working in Africa and Asia during the time-frame in which the concept emerged.	Requested information from respondents about their recollections of the context in which they first encountered the term mosaic habitats. Provided key sources, people and localities to be further investigated.
Book index search: Consulted over 200 books covering a range of topics (ecology, palaeoenvironments and human evolution) published between approx. 1916-2013. Indexes were checked for a predefined range of terms, relating to habitats and environments. These were: *environment; habitat; mosaic, heterogeneity, heterogeneous* and *patchiness*, as well as combinations of these.	Key texts, in particular early textbooks and conference proceedings were examined for associated references in an effort to identify the texts most influential in popularizing the term 'mosaic'.

Table 2: Principal historical sources used in this study to track the development of the 'mosaic habitat' concept within paleoanthropology

Table 3:

Question 1	What is the first paper that you remember discussing mosaic habitats in the context of the hominin record (rather than in the ecological literature)? Please give bibliographic details, if possible.
Question 2	When do you first remember hearing about mosaic habitats in relation to hominin evolution? Was it at a conference, seminar or meeting? If so, can you remember the speaker, and the date and place of the meeting?
Question 3	As pictures have been key in promoting human evolution in books and museum displays, is there a picture or diorama that you think encapsulates the idea of a mosaic habitat? Please could you tell us where or what it is? And is there an earlier example?

Table 3: E-mailed questions sent to senior academics to obtain first-hand information about the development of the 'mosaic habitat 'concept.

Figure 1:

Figure 2:

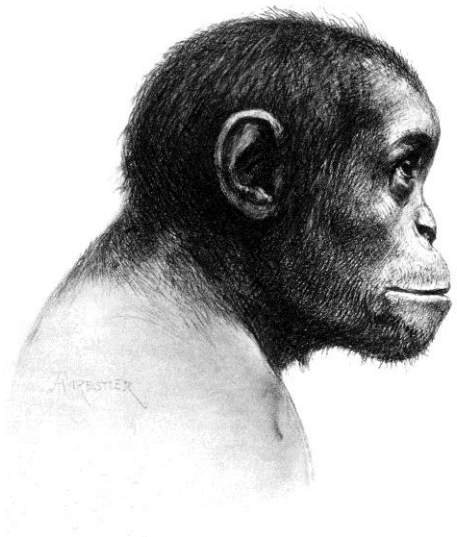


Figure 3:

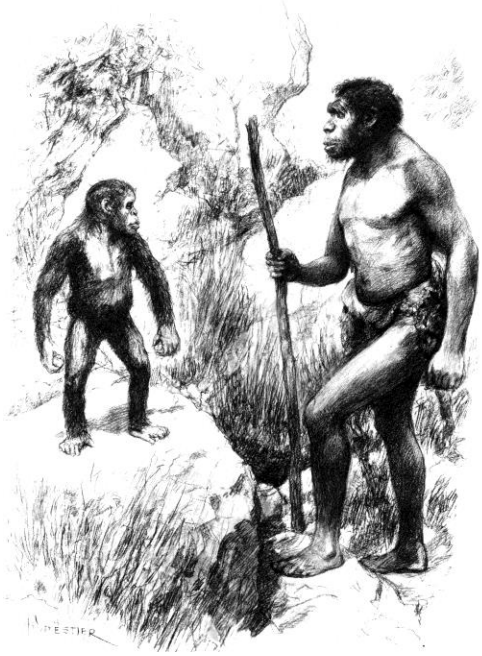


Figure 4:

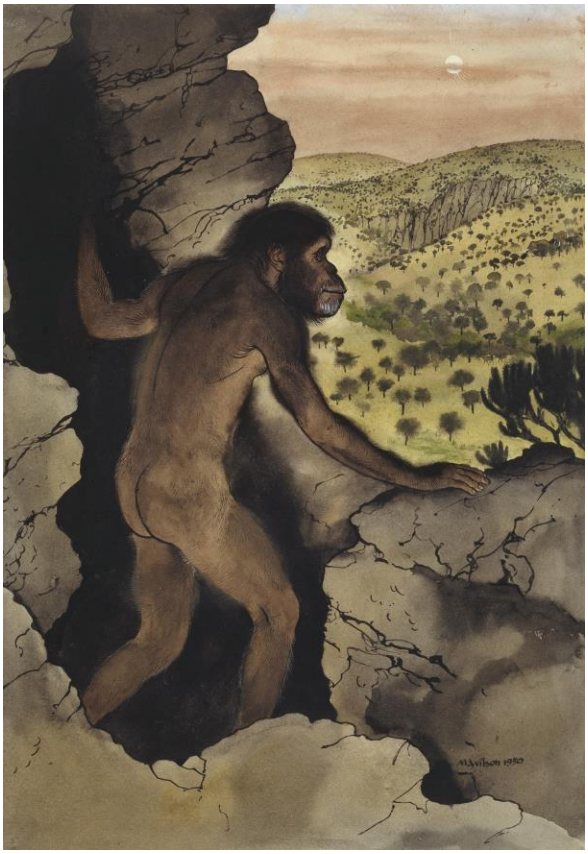


Figure 5:

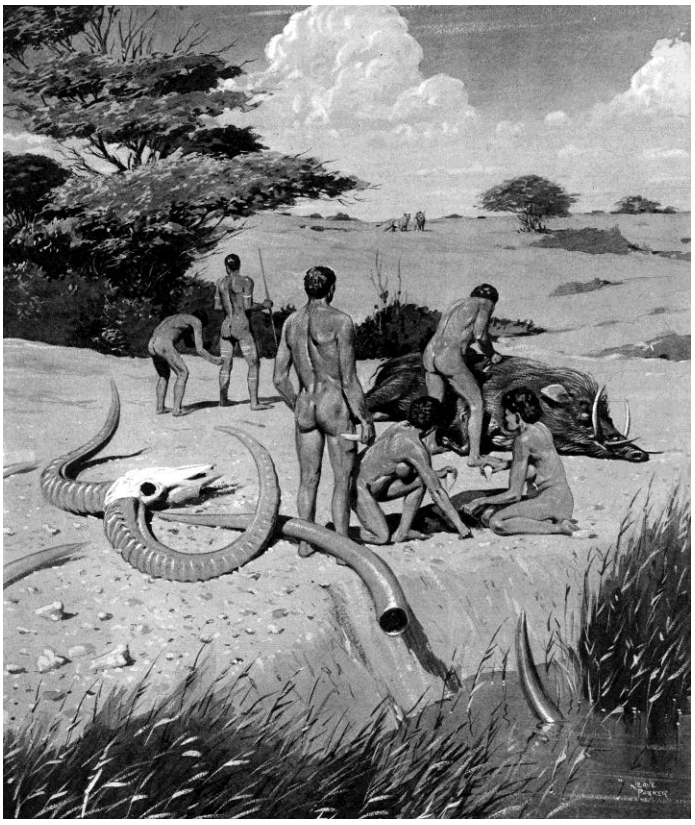
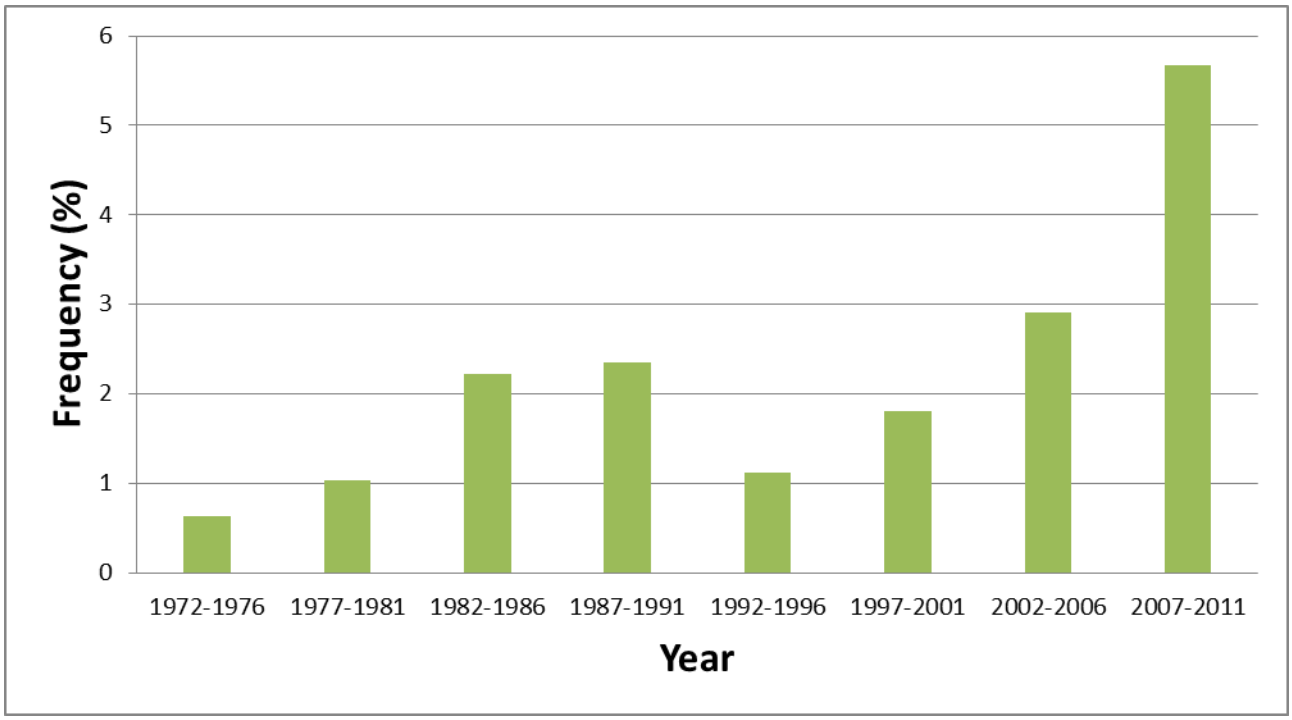


Figure 6:


Frequency (%)
6
5
4
3
2
1
0
1972-1976
1977-1981
1982-1986
1987-1991
1992-1996
1997-2001
2002-2006
2007-2011
Year